Climate change and the koala *Phascolarctos cinereus*: water and energy

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ABSTRACT

We studied two groups of koalas during a drought in central Queensland to investigate potential impacts of climatic variability on the physiology and behaviour of this species. The tree use, water turnover, field metabolic rate and diet of koalas during autumn and spring were compared to a similar study of koalas in summer and winter, also in central Queensland, to generate a seasonal picture of the response of koalas to climatic variation. We also compared the microclimate temperature of a range of food and non-food tree species against daily ambient temperatures, to examine the benefit to koalas of using of non-food species. Field metabolic rate, adjusted for body mass, was significantly higher in spring than autumn and there was no difference between males and females. Neither females with pouch young nor those with back young had significantly different FMR to that of females without young, confirming that koalas may compartmentalize energy demands during lactation. Estimations of theoretical water influx, determined from FMR of koalas, were generally lower than water flux determined by tritiated water turnover. This mismatch could indicate that koalas are able to modify their assimilation of energy from browse in order to maximize water intake. Temperature was generally lower in non-food trees used by koalas in daytime than in the food trees, which were generally used at night. Leaf moisture may influence tree selection during periods of extremely high or low temperature, but the physical attributes of trees, such as their capacity to "buffer" koalas against extremes of ambient temperature, appear to be important to selection by koalas. We conclude that koalas adapt their behaviour, using shady trees during the day, but might also employ physiological adaptations, to access sufficient water for evaporative cooling during periods of hot, dry weather.

Key words: Koala, Temperature, Field Metabolic Rate, Water Turnover

Introduction

Climate change could alter the physiological relationship of animals to their environment, by influencing vegetation associations and structure, affecting variation and duration of temperature or humidity events or through a range of flow-on effects, such as influencing other animals' distribution. Koalas *Phascolarctos cinereus* are widely, but unevenly, distributed across Queensland, and frequently associated with habitat patches that have survived agricultural development and, towards the coast, urban or industrial development. The majority of koalas that occur in Queensland do so outside of the south east bioregion (AKF 2009), in which area they are classified as vulnerable; elsewhere they are considered as common protected wildlife under the *Nature Conservation Act* (Qld) 1992.

Koalas at the north and west of their range probably occur at the limit of their physiological capacity to endure drought and heat, so those koalas might be expected to adopt behavioural strategies that minimise their exposure to microclimate extremes. In such environments, the frequency, intensity and duration of extreme temperatures, drought and humidity determine survivorship by influencing environmental water availability, metabolic water balance, temperature regulation and foliage availability (Specht and Specht 2002). Climate change predictions include reduced rainfall and increased temperatures and duration of drought across the range of the koala in Queensland (Hughes 2003), which would exacerbate the impact of continued landscape clearing, habitat fragmentation and altered availability of surface and shallow aquifers.

Subsisting primarily on a diet of *Eucalyptus* foliage, koalas' persistence in any area is inexorably linked to the survival of patches of *Eucalyptus* trees, to the extent that habitat has been rated for koala suitability with emphasis on the existence of browse species (McAlpine *et al.* 2007). This approach may not always be adequate, since the koalas' tree use goes beyond simply moving between food trees (Clifton *et al.* 2007; Kavanagh *et al.* 2007; Tucker *et al.* 2007). Further, suitable browse species are far more widely distributed than koalas (e.g. *E. camaldulensis* McDonald *et al.* 2009). Since the major source of cooling for koalas is evaporative water loss from the respiratory tract (Degabriele and Dawson 1979), the koala's water balance has been a target of considerable attention to those interested in the ecological amplitude of this species (Krockenberger 2003). The water content of browse represents the major component of water influx for koalas

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(Degabriele *et al.* 1978; Nagy and Martin 1985), so it was not surprising that some workers concluded water content of leaves to drive tree selection by koalas at warmer times of year (Ellis *et al.* 1995). Since riparian trees were found to have highest leaf moisture in central and north western Queensland (Ellis *et al.* 1995, Munks *et al.* 1996) it follows that conservation of these areas, which also house the densest aggregations of koalas in drier areas of Queensland (Munks *et al.* 1996, Sullivan *et al.* 2003; 2004), should deliver the best outcome in terms of long term koala persistence.

Gordon *et al.* (1988) describe the impact of drought and extreme heat on riparian vegetation and the consequent collapse of the resident koala population in southwestern Queensland. A similar story appears to have unfolded in central Queensland. The works of Gordon *et al.* (1990) and Melzer (1994) provide details of a long-term study of a koala population at Springsure, central Queensland. These authors monitored population dynamics across several seasons from 1970 to 1994. Melzer (1994) surveyed koala population density at five contrasting habitats around Springsure. Population density ranged from <0.2 to 0.4 koalas/ha. Four of the five sites were resurveyed in autumn and spring 2009 following repeated anectdotal accounts of extensive tree death and koala mortality. Koalas could only be located at the site which formally had the densest population (0.02 koalas/ha: formerly 0.4 koalas/ha) and at one other site only very isolated traces could be located (<0.01 koalas/ha: formerly 0.2 koalas/ha). The riparian *E. tereticornis* and *Corymbia tessellaris*, around which the densest aggregation of koalas occurred, had declined with extensive tree death.

Where left uncleared, the vegetation on the adjacent plains and slopes, which historically supports fewer koalas (Melzer 1994), has survived and koala numbers in these areas do not appear to have suffered a similar fate to their riparian-dwelling conspecifics. At Blair Athol, some 200 km north of Springsure, koalas have persisted throughout the dry period on the *E. populnea* and *E. crebra* dominated woodland plains as well. This outcome suggests that concentrating conservation efforts on the riverine communities may not always deliver the best outcome for koalas, if those areas were more susceptible to a general drying of the environment over time. Sullivan *et al.* (2004) also observed that almost 50% of the koalas in the mulgalands occurred outside of the riverine systems, so we re-visited the data that were compiled for Springsure and repeated the investigation at Blair Athol during different seasons of the year to generate a seasonal picture of the metabolic requirements of the koalas. Koalas at both Springsure and Blair Athol use their habitat in a similar fashion to other Queensland koalas – a proportion of their daytime tree use occurs in non-food species (Ellis *et al.* 2002b). This behaviour may be due to a range of factors, including social influences and predator avoidance that are difficult to quantify over a short period of time. In this study, we test the hypothesis that there is an energetic benefit to koalas of moving from the food trees into non–food trees for daytime resting. If such a benefit exists, as a result of shade for example, this would help explain the role of non-food trees in the ecology of koalas in Queensland and provide another useful element to assessing habitat quality for koalas.

Methods

Study Site

Blair Athol Coal Mine is located in the Brigalow Belt of central Queensland (22.685S 147.592E). The 3000-hectare Blair Athol site is approximately 25 kilometres north-west of Clermont. The climate is sub-humid; average minimum and maximum temperatures for autumn (March) are 19.4 °C and 32.1 °C and for spring (September) and 12.0 °C and 28.8 °C respectively and the average annual rainfall is 662 mm (Bureau of Meteorology 2008). The predominant plant communities are *Acacia rhodoxylon* / *Eucalyptus crebra* and *E. populnea* / *E. melanophloia* woodlands. Patches of E. tereticornis are present and the area supports a low density population of koalas (1 koala per 100 ha, Ellis *et al.* 2002a).

Study Animals

Koalas at Blair Athol Coal Mine for which tree use and diet (Ellis *et al.* 2002b) and breeding dynamics (Ellis *et al.* 2002a) have been previously described were the subject of the current research and the leaf moisture and diet results previously reported (Ellis *et al.* 2002b) are supplied as Table 1. These koalas (average mass males 6.7 kg; females

Table 1. Tree species represented in the diet of koalas at Blair Athol and leaf moisture.

Tree species	Spring		Autumn	
	Diet (%)	Moisture (%)	Diet (%)	Moisture (%)
E. populnea	59.0 ± 15.8	48.6 ± 2.2	58.8 ± 29.6	66.0 ± 7.9
E. crebra	13.9 ± 22.2	45.9 ± 2.6	6.0 ± 17.0	64.1 ± 6.7
E. tereticornis	8.7 ± 10.8	48.6 ± 2.2	5.4 ± 5.5	61.7 ± 7.0
E. melanophloia	3.3 ± 3.4	48.9 ± 2.6	0.0	68.6 ± 7.1
E. cambageana	3.1 ± 2.8	53.0 ± 2.7	1.9 ± 3.9	68.8 ± 1.1
C. dallachiana	0.5 ± 1.8	53.6 ± 2.0	2.5 ± 4.9	64.5 ± 7.8
M. bracteata	0.4 ± 0.9	39.1 ± 4.1	0.0	61.4 ± 16.6
New growth (not identified)	1.8 ± 3.4	nr	25.2 ± 25.6	nr
Other species	11.0 ± 9.6	nr	0.25 ± 0.7	nr

nr: not recorded

5 kg) range around the mine area, on the lease itself and on adjacent grazing, farming and undisturbed property and state forests. The results for winter (July) and summer (December) at Springsure, used for comparison, were as reported in an earlier study (Ellis *et al.* 1995).

Analysis of water turnover (WTR) and field metabolic rate (FMR)

Five male and nine female koalas were captured for analysis of FMR using doubly labelled water in September (4 male and 7 female) and Autumn (4 male and 7 female). Three males were sampled on both seasons and 5 females were sampled in both seasons. Each animal was weighed and a 2 ml blood sample collected by cephalic venipuncture. Tritiated water (0.5 ml, 370 MBq/ml) followed by 1.0 ml oxygen-18 (97% atoms excess) was infused through the same needle to the cephalic vein, and the animal placed in a 2m x 1m x 0.5m aluminium cage in a shaded place for at least 2 h (Ellis and Carrick 1992). Then another 2 ml blood sample was taken and the koala released into the tree from which it had been caught. After 7 to 11 days, the koalas were recaptured, weighed and a second 2 ml blood sample was collected.

The blood samples were collected in 5 ml sterile vials and frozen at -20°C. These samples were then analysed as described by Ellis *et al.* (1995).

Theoretical water influx

The diet of each koala included in WTR and FMR experiments in both seasons was determined using faecal cuticle analysis and leaf moisture content was determined for each browse species at the site. These results have been previously reported (Ellis *et al.* 2002b) and are summarised here in Table 1. The contribution of each diet species to the diet of each koala was used to determine the amount of dietary water available to each koala for the current study.

It has been estimated that eucalypt leaves (*E. ovata*) contain 20.1 kJ per gram of dry matter and that koalas extract 45% of the energy of their diet (Nagy and Martin 1985). Thus 1 g of dry matter will yield 9.05 kJ and the amount of dry matter ingested each day can be determined from the calculations of CO_2 production made during doubly labelled water analysis. Metabolic water was estimated using the conversion factor of 0.0307 mL of H_2O produced per kJ energy released (Nagy and Martin 1985). Theoretical water influx for each koala was therefore derived from leaf moisture values of the dietary components as indicated by faecal pellet analysis and estimates of dry matter intake and metabolic water production. In simple terms, by knowing the quantity of leaf required to satisfy FMR and combining this information with accurate information on the water content of the ingested leaf, we calculated a theoretical water influx to compare with that determined using tritiated water turnover.

Tree temperature and ambient temperature

Ten individual adult trees of each of 4 species used by koalas (*E. populnea*, *E. cebra*, *M. bractata* and *A. harpohylla*) were selected for daytime temperature measurement. These trees were spread across the range of radio–tracked koalas at Blair Athol. A temperature transmitter (Titley Electronics, Ballina, N.S.W.) was attached, in a protective screen, on the south side of the trunk directly beneath the first branch that was above 3 m from the ground for each tree to be sampled. Two trees of each species were selected each day making a total of 8 trees measured each day, with the recording equipment moved to a different 8 trees on subsequent days until all 10 trees of each species were measured, over a five-day period during summer 2002. Temperature was recorded remotely using a pulse period meter (Titley Electronics, Ballina, N.S. W.) attached to a Regal 2000 VHF receiver (Titley Electronics, Ballina, N.S.W.) every 2 h between dawn an dusk of each of the five days. Ambient temperature was recorded at a weather station on the Blair Athol Coal Lease, located centrally between the tree recording locations.

Comparison with Springsure data

Data collected at the Springsure, central Queensland, site (as reported in an early study by Ellis *et al.* 1995) were incorporated for comparison of FMR and water turnover. Although diet analysis was not conducted during that study, leaf moisture results for the species that koalas were found in were included as the best estimate for water availability in the diet of these koalas (Krockenberger 2003), to estimate theoretical water influx.

Statistical analyses for Blair Athol koalas were performed using repeated measures ANOVA. Although this excludes those koalas that were not used in both seasons, this avoids the complication of lack of independence of data. FMR of koalas was scaled according to $Mass^{0.75}$ for consistency with Ellis *et al.* (1995). For comparisons across both sites, single factor ANOVA, t tests and paired t tests (for comparison of theoretical and actual water turnover) were used for groups with equal variances.

Results

Analysis of water turnover and field metabolic rate

At Blair Athol, average water turnover was not significantly different between season for those koalas sampled in both seasons (repeated measures ANOVA: $F_{1,6}=1.21$; $P=0.31$), nor was there any difference between sexes within either season ($F_{1,6}=0.31$; $P=0.60$).

Field metabolic rate at Blair Athol, adjusted for body mass was significantly higher in spring (346.47 ± 11.4 kJ $kg^{0.75}$ day^{-1}) than autumn (290.62 ± 12.9 kJ $kg^{0.75}$ day^{-1}, repeated measures ANOVA; $F_{1,6}=11.10$; $P=0.02$, Table 2). There was no difference between males and females ($F_{1,6}=1.37$; $P=0.29$). Neither females with pouch young (n = 3) nor those with back young (n = 3) had significantly different FMR to that of females without young, although the sample size was small.

Female koalas at Blair Athol had significantly lower FMR in autumn ($t_8 = 2.63$, $P<0.05$), but not spring ($t_8 = 1.76$, $P<0.1$) than recorded for their counterparts in Victoria during winter (Nagy and Martin 1985).

Table 2. Mass, field metabolic rate (FMR) and water turnover rate (WTR) of koalas at Blair Athol, central Queensland, in spring and autumn.

Koala	Sex	Spring			Autumn		
		Mass (kg)	FMR (kj kg$^{-0.75}$ day^{-1})	WTR (mL kg$^{-0.8}$ day^{-1})	Mass (kg)	FMR (kj kg$^{-0.75}$ day^{-1})	WTR (mL kg$^{-0.8}$ day^{-1})
8251	m	7.0	360.0	58.26	8.0	264.0	66.25
8252	f	5.5	303.7^{by}	49.08			
8253	m	7.0	283.4	47.22	6.0	227.6	48.80
8254	f	6.2	327.8	37.39	5.8	340.2	65.65
8255	f	5.2	339.7^{by}	42.34	5.8	306.9^{py}	57.99
8258	m	8.0	402.1	42.74			
8259	f	4.5	347.5	54.20	4.	221.4	59.41
8260	m	5.0	368.5	59.83	6.	281.5	52.76
8268	f	5.9	382.4	44.71			
8269	f	2.5	318.5	63.00	4.0	330.1	57.93
8278	f	5.2	377.7^{by}	46.50	6.5	301.6^{py}	45.77
8279	m				7.5	339.4	59.55
8280	f				5.5	279.7^{py}	59.50
8281	f				3.0	304.4	62.34
Average			346.47	49.57		290.62	57.81
SE			11.41	1.94		12.90	2.47

Legend: ^{by} back young present, ^{py} pouch young present, nr: not recorded

Theoretical water influx

Consumption of dry matter and theoretical water influx were calculated for individual koalas that were sampled in both seasons at Blair Athol (Table 3). Since dry food consumption was calculated directly from FMR the pattern of change was identical to that of FMR. For the determination of theoretical water turnover two more variables were involved (consumption of species and leaf moisture), but there was still a significant effect of season on theoretical water turnover ($F_{1,6}$=23.13; P=0.003) and no effect of sex ($F_{1,6}$=2.18; P=0.19), in line with the differences in FMR (Figure 1).

Theoretical water influx derived from FMR was compared with actual water influx, as estimated by tritiated water turnover and paired t tests revealed theoretical water influx to underestimate actual water influx in spring (t_7=2.87; P=0.02), winter (t_4 = 5.9, P = 0.004) and summer (t_5 = 3.91, P = 0.01) but to approximate this value in autumn (t_7=1.19; P=0.27, Figure 1).

Tree temperature and ambient temperature

There was disparity between the temperature recorded within the microclimate of several tree species in response to increasing day-time temperature; *E. populnea* responded to temperature according to the regression equation:

Table 3. Dry matter intake, theoretical water influx (Water in) and water turnover rate (WTR) for koalas at Blair Athol, central Queensland. Dry matter intake was estimated from field metabolic rate. Theoretical water influx was estimated from dry matter intake and leaf moisture content of species represented in the browse as determined by faecal pellet analysis.

Koala	Sex	Spring			Autumn		
		Dry matter (g kg$^{-0.75}$ day^{-1})	Water in (mL kg$^{-0.8}$ day^{-1})	WTR (mL kg$^{-0.8}$ day^{-1})	Dry matter (g kg$^{-0.75}$ day^{-1})	Water in (mL kg$^{-0.8}$ day^{-1})	WTR (mL kg$^{-0.8}$ day^{-1})
8251	m	39.8	45.2	58.3	29.2	55.6	66.3
8253	m	31.3	35.1	47.2	25.2	51.2	48.8
8254	f	36.2	41.2	37.4	37.6	77.2	65.7
8255	f	37.6	41.9	42.3	33.9	67.3	58.0
8259	f	38.4	44.2	54.2	24.5	49.0	59.4
8260	m	40.7	47.2	59.8	31.1	58.4	52.8
8269	f	35.2	43.2	63.0	36.5	67.7	57.9
8278	f	41.8	45.5	46.5	33.4	61.7	45.8
Average		37.6	42.9	51.1	31.4	61.0	56.8
SE		1.3	1.4	3.4	1.8	3.6	2.8

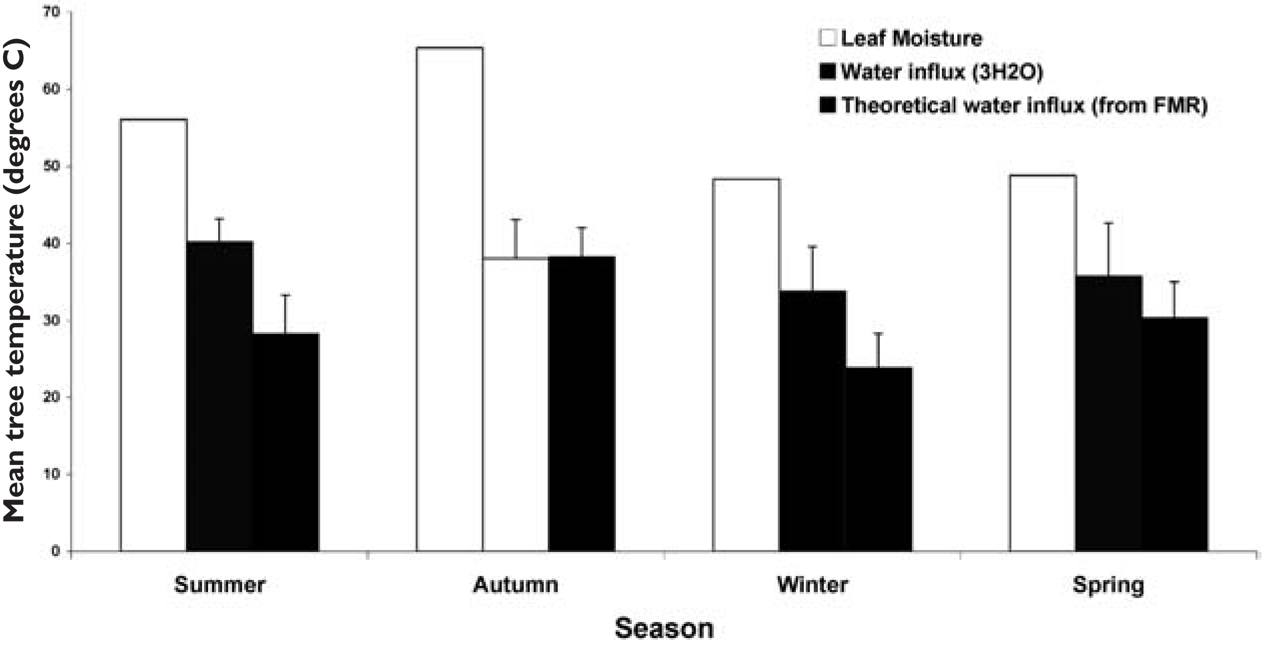

Figure 1. Leaf moisture (% by mass) of browse , water influx of koalas (ml per kg$^{-0.75}$) measured using tritated water dilution ("3H2O") and derived from FMR values (also ml per kg$^{-0.75}$, "Theoretical"). Values are for Blair Athol in autumn and spring and Springsure in summer and winter.

$$y = 0.8691x + 6.7835 \ (R^2 = 0.9531)$$

and *M. bracteata* (tea-tree) responded according to the equation:

$$y = 0.6254x + 11.94 \ (R^2 = 0.9789).$$

Where y is temperature recorded in the tree and x is ambient day temperature recorded under standardised conditions (Figure 2).

The slopes for both food species investigated (*E. populnea* and *E. crebra*) were greater than those for the non-food species (*A. harpophylla and M. bracteata*), indicating a closer relationship to day temperature within the canopy of the food species and a greater disparity between the temperature recorded within non-food and food trees as ambient temperature increased.

Discussion

Analysis of water turnover and field metabolic rate

The koala's reliance on browse moisture to meet its water requirements has been the subject of several reports (for review see Ellis *et al.* 1995) and the animal has recently been credited with a capacity to compartmentalize its energy demands to allow adaptive flexibility in response to the demands of lactation (Krockenberger 2003). The latter of these concepts suggests that koalas are not precariously placed with regard to metabolic costs and energy intake; so our strict interpretation of the consequences of water turnover and metabolic rate for this species may need to be revisited.

Our data support the conclusions of Krockenberger (2003), that female koalas can offset the metabolic cost of lactation (or indeed the raising of young) through particular behavioural and physiological adaptation (Table 2). Our measurements of mothers with young were in the relatively benign (neither very hot or very cold) periods of spring and autumn, but this result still adds weight to the argument that koalas can modify, behaviourally, their energetic demands. In his 2003 work, Krockenberger found that while the measured cost of lactation was negligible for koalas, this was due to a compartmentalization or compensation of energetic expenditure by lactating koalas, which ate more food with relatively higher energy (and relatively lower water). For example, substituting the cost of producing milk for the mother with the benefit of thermoregulation provided by the young during cooler months, the costs of lactation could be offset.

That FMR of female koalas at Blair Athol was lower than reported for females in Victoria during winter is unsurprising, being commensurate with a more benign nature of autumn in central Queensland. The result may indicate that the animals in the current study were encountering comparatively thermoneutral temperatures and further confirms that the effect of environmental variations outside of the thermoneutral zone of koalas, which were postulated by Ellis *et al.* (1995) to influence tree selection by koalas, were absent during the present study.

Theoretical water influx

We have previously reported that increases in leaf moisture of diet species do not necessarily result in proportional increases in the occurrence of these species in the diet of koalas (Ellis *et al.* 2002b). Indeed, for the most frequently eaten species (*E. populnea*) at this study site, percent occurrence of the species in the diet of koalas was lower at that period of the year when leaf moisture of this species was highest (autumn, Ellis *et al.* 2002b); a result inconsistent with the assertions of Ellis *et al.* (1995), who found leaf moisture and daytime tree selection to be positively correlated.

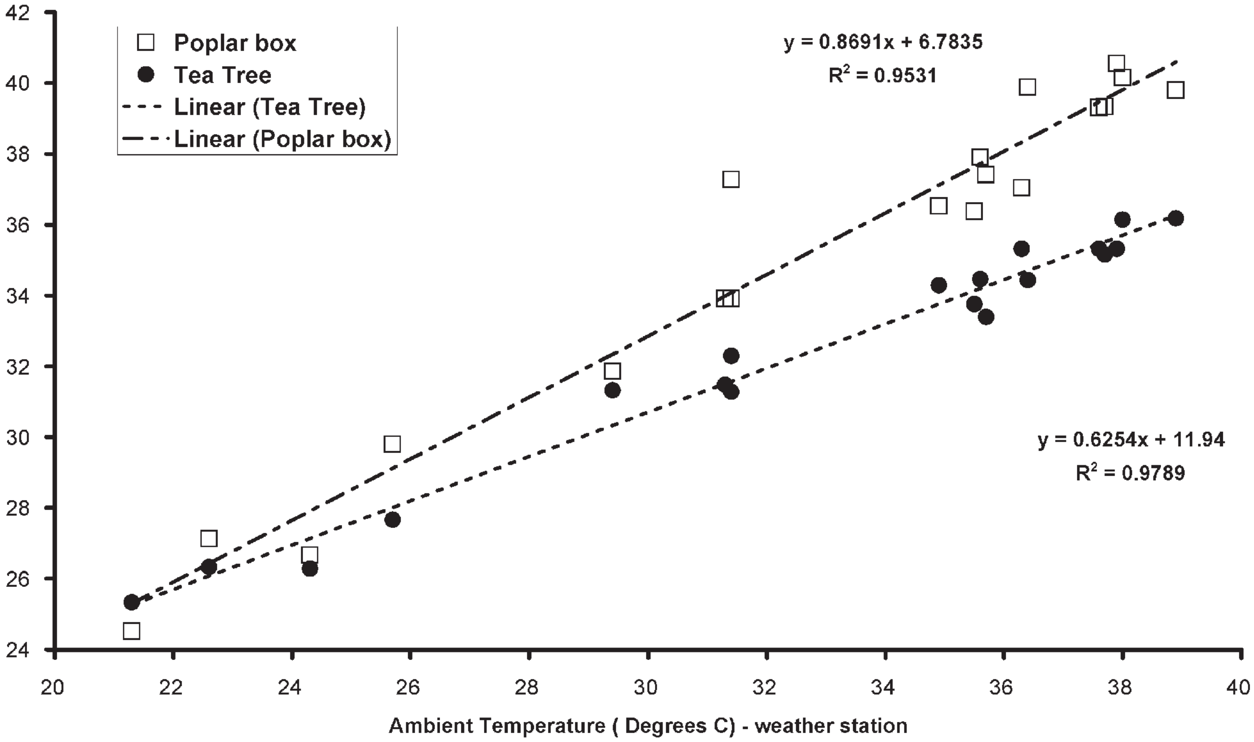

Figure 2. Comparison of mean temperature recorded in *E. populnea* (Poplar box) and *M. bracteata* (Tea Tree) with mean day temperature recorded at a weather station at Blair Athol in summer.

Nagy and Martin (1985) and Ellis *et al.* (1995) found theoretically derived water influx rates to slightly underestimate water influx, leading both reports to suggest the possibility for koalas to drink free water. Indeed, koalas have been observed drinking free water from the stems and branches of trees after periods of rain at Springsure (A. Melzer pers obs). In spring, FMR was high (Table 2) and leaf moisture was low (Table 1) so a relatively lower water turnover with high FMR is not unusual.

When considered in light of the work of Krockenberger (2003) and Clifton *et al.* (2007), the disparity between water turnover estimated from (a) combination of FMR calculations and leaf moisture content; and (b) water turnover determined by tritiated water turnover, might indicate that koalas can adjust their assimilation of energy from their diet. The report by Logan and Sanson (2002), in which it was argued that Victorian koalas could compensate for decreased feeding efficiency that resulted from advanced tooth wear by eating a greater quantity of food, is relevant here. If water is the principal determinant of the quantity of *Eucalyptus* leaves that need to be consumed rather than energy, then koalas might modify the digestion of leaf "dry matter" and consequential energy intake for a given quantity of leaf material while obtaining the required quantity of water. If koalas can adjust the particle size and passage rate of their ingested food in order to meet energy demands (Krockenberger and Hume 2007), then perhaps they could also do this to meet water demands. Our calculations of FMR represent the minimum quantity of dry food that would need to be consumed to meet CO_2 production, as measured using the doubly labelled water technique. If the conclusions for Victorian koalas (Logan and Sanson 2002) can be extended to this situation, then koalas in Queensland facing high water demands would already have a mechanism to obtain their water requirements without the need to assimilate "surplus" quantities of food - in other words water intake and energy intake can be decoupled. This mechanism could be mediated in the caecum, since it is known that particles of different sizes are separated for different rates of passage through the gut of the koala (Cork and Warner 1983). If true, it could be predicted that koalas under water stress should produce larger particles in the faeces and the energy content of faeces should vary, depending on energy and water requirements of koalas in hot and dry versus cool and wet conditions. This sort of digestive flexibility has already been alluded to by Krockenberger and Hume (2007), with regard to energy intake by lactating female koalas. For the compartmentalisation and compensation of energetic costs described by Krockenberger (2003) to exist, there must be some "room to move" in koala energetics. If this is the case, then water balance, not nutritional requirements, could be the range-limiting factor in koala distribution.

This also means that the disparity between water intake determined using FMR techniques and actual water turnover might not result from koalas consuming free water, as previously postulated (Nagy and Martin 1985; Ellis *et al.* 1995). Even under conditions of water stress, koalas (although probably choosing leaves with the highest leaf moisture (Melzer 1994)) might not drink free water, but rather might shift the balance of water ingestion to energy assimilation in their diet. Bouts of eating by koalas at times of the day when leaves are not maximally hydrated would still yield lower water influx values for those koalas than would apply at times of maximum leaf hydration. Specific selection of the most succulent leaves and opportunistic drinking of free water (eg. dew or precipitation on leaves) would also still result in higher than theoretically predicted water influx. Such conclusions, however, are still speculative given that the energy content of leaves consumed in the present study were not specifically measured; we have relied on previous work based on other *Eucalyptus* species. Further, the effect of lactation on energy balance of females needs further examination (Krockenberger and Hume 2007), because the inclusion of lactating females in the present study probably includes animals that are exporting energy through milk to their joeys.

Tree temperature and ambient temperature

Although some preliminary work has indicated that there are advantages for koalas to use non-food tree species (Pfeiffer *et al.* 2005) this behaviour appears only recently to have generated interest. In N.S.W., two recent studies have commented on the use by koalas of non-food species (Kavanagh *et al.* 2007; Matthews *et al.* 2007), with Kavanagh *et al.* (2007) suggesting that there may be a relationship between the use of these trees and severe weather events. At other sites, such as St Bees Island, in central Queensland, tree use was attributed to social dynamics as well as tree characteristics (Ellis *et al.* 2009). Our data indicate that to cope with extremes of temperature, koalas at Blair Athol use the non-food tree species for shelter and this probably constitutes an adaptation to an otherwise unsuitable environment. This pattern of use was recorded away from the riverine vegetation communities in the area: whether koalas in the *E. coolibah* dominated alluvial landforms and *E. tereticornis* dominated creek systems display similar behaviour is unknown. As day temperature increases, the thermoregulatory advantage to koalas of using the tea tree and brigalow trees appears to increase (Figure 2), so it is likely that more use would be made of these trees in hotter weather. On this basis, it appears likely, at least for the non-riverine systems, that non-food trees would be as critical to the persistence of koalas as would be the food trees.

In the time since the Springsure study was undertaken (1995), that population, particularly the riparian elements, has suffered a severe decline (Melzer unpublished data). This has coincided with the death of many of the trees on which koalas relied in the creek systems. Koalas have maintained the sparse distribution outside of these creek systems, in a similar distribution to that reported by Melzer (1994) and to that existing at the Blair Athol site (Ellis *et al.* 2002b). Previous reports of koala population declines on creek lines note the defoliation of trees accompanying extreme drought (Gordon *et al.* 1988) and consider that mortality is associated with adverse weather conditions when large numbers of koalas occur in sub-optimal habitat (Gordon *et al.* 1990). Areas of creek lines where surface water persists through drought periods are considered to be the optimal habitat (Gordon *et al.* 1990), but with modified land use (removing water for agriculture) and severe drought, even these locations may fail to support the trees on which koalas depend. As a result, future determinations of what constitutes the best habitat for koalas may need to consider the drought-adaptation of the tree species that are present.

During the Springsure study, water-limiting conditions probably drove leaf selection by koalas in summer. Such water-limiting conditions may not have been present during the other seasons we compared at Springsure or Blair Athol. As a result, our conclusion (based on the Springsure work) that leaves of greater moisture content would be selected during warmer and drier periods at Blair Athol (Ellis *et al.* 2002b), was not supported, perhaps because the pressures driving this selection were absent.

Conclusions

We postulate that a complex behavioural and physiological interaction between the koalas and the tree species they use exists, influencing species utilisation by koalas in heterogenous landscapes. The individual characteristics of a tree, such as its microclimate, which may have a profound effect on the FMR of koalas that utilise it, may ultimately be as influential to the selection of species and individual trees by koalas as features such as leaf moisture. The costs of movement from food trees to non food trees, which include energy expended for movement and exposure to predation, must be offset by the thermoregulatory benefits of resting in the non food trees.

Comparing our work with the recent investigation of the water relations of koalas in the north of their range (Clifton *et al.* 2007) suggests that there is more than one model of koala ecophysiology that needs to be considered when planning for the conservation of this species.

In the tropical moist environment, koalas occur in patchy but dense populations, with distribution impacted by development for agriculture and human habitation. In that environment there appears to be a single habitat model: high water demand and high shade requirement (Clifton *et al.* 2007). These areas experience higher temperatures and higher summer and autumn rainfall patterns.

The subtropical subhumid inland Queensland environment supports a patchy distribution of koalas impacted mainly by agricultural development. From the work of Sullivan *et al.* (2003) there are three koala habitat models to be considered:

The first is the riverine communities that exist as a high affinity – high capacity system; they attract and support high-density koala populations. The second are the woodland areas that operate as a high capacity but low affinity system: they contain about half of all the koalas in an area, in a low density. The third system is the plains that have low capacity and low affinity for koalas.

How each of these systems is impacted by, or more importantly responds to, the effects of climate change could guide management decisions designed to conserve koala habitat in the future.

Because the high affinity-high capacity riverine systems appear to hold the greatest number of koalas in the smallest area, they appeal for conservation purposes as they should be relatively cheap to conserve and will save the most individuals. However, before resources are invested in these systems for conservation of koala habitat, we need to understand whether it is the habitat with the greatest capacity for koalas in mild weather periods, or the habitat with the greatest ecological plasticity over time that will be most likely to survive the serious environmental changes we may face under current climate change predictions.

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References

Australian Koala Foundation. 2009. Distribution Map at: https://www.savethekoala.com/koalasdistribution.html

Bureau of Meteorology. 2008. Commonwealth Bureau of Meteorology. http://www.bom.gov.au/.

Clifton, I.D., Ellis, W.A.H., Melzer, A. and Tucker, G. 2007. Water turnover and the northern range of the koala (*Phascolarctos cinereus*). *Australian Mammalogy* **29**, 85-88.

Degabriele, R. and Dawson, T.J. 1979. Metabolism and heat balance in an arboreal marsupial the koala (*Phascolarctos cinereus*). *Journal of Comparative Physiology* **134**, 293-301.

Degabriele, R., Harrop, C.J.F. and Dawson, T.J. 1978. Water metabolism of the koala. In 'The Ecology of Arboreal Folivores'. (Ed. GG Montgomery) pp. 163 - 172. (Smithsonian Institute Press: Washington, D.C.)

Ellis, W.A.H., Bercovitch, F.B. and Melzer, A. 2009. Spatiotemporal dynamics of habitat use by koalas: the checkerboard model. *Behavioral Ecology and Sociobiology* 63:1181–1188.

Ellis, W. and Carrick, F.N. 1992. Total-Body Water and the Estimation of Fat in the Koala (*Phascolarctos cinereus*). *Australian Veterinary Journal* **69**, 229-231.

Ellis, W.A., Hale, P.T. and Carrick, F. 2002a. Breeding dynamics of koalas in open woodlands. *Wildlife Research* **29**, 19-25.

Ellis, W.A.H., Melzer, A., Carrick, F.N. and Hasegawa, M. 2002b. Tree use, diet and home range of the koala (*Phascolarctos cinereus*) at Blair Athol, central Queensland. *Wildlife Research* **29**, 303-311.

Ellis, W.A.H., Melzer, A., Green, B., Newgrain, K., Hindell, M.A. and Carrick, F.N. 1995. Seasonal variation in water flux, field metabolic rate and food consumption of free-ranging koalas (*Phascolarctos cinereus*). *Australian Journal of Zoology* **43**, 59-68.

Gordon, G., Brown, A.S. and Pulsford, T. 1988. A koala (*Phascolarctos cinereus* Goldfuss) population crash during drought and heatwave conditions in south-western Queensland. *Australian Journal of Ecology* **13**, 451-461.

Gordon, G., McGreevy, D.G. and Lawrie, B.C. 1990. Koala populations in Queensland: major limiting factors. In *Biology of the koala.* (Eds A.K. Lee, K.A. Handasyde & G.D. Sanson), pp 85-95. (Surrey Beatty and Sons Pty Ltd, Chipping Norton, NSW).

Hughes, L. 2003. Climate change and Australia: Trends, projections and impact. *Austral Ecology* **28**, 423 - 443.

Kavanagh, R.P., Stanton, M.A. and Brassil, T. 2007. Koalas continue to use their previous home-ranges after selective logging in *Callitris-Eucalyptus* forest. *Wildlife Research* **34**, 94-107.

Krockenberger, A. 2003. Meeting the energy demands of reproduction in female koalas, *Phascolarctos cinereus*: Evidence for energetic compensation. *Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology* **173**, 531-540.

Krockenberger, A.K. and Hume, I.D. 2007. A flexible digestive strategy accommodates the nutritional demands of reproduction in a free-living folivore, the Koala (*Phascolarctos cinereus*) *Functional Ecology*, 21(4), 748-756

Matthews, A., Lunney, D., Gresser, S. and Maitz, W. 2007. Tree use by koalas (*Phascolarctos cinereus*) after fire in remnant coastal forest. *Wildlife Research* **34**, 84-93.

McAlpine, C., Rhodes, J., Peterson, A., Possingham, H., Callaghan, J., Curran, T., Mitchell, D. and Lunney, D. 2007. Planning guidelines for koala conservation and recovery. A guide to best planning practice. Australian Koala Foundation and The University of Queensland, also available at http://espace.library.uq.edu.au/view/UQ:124088', Brisbane.

McDonald, M.W., Brooker, M.I.H. and Butcher, P.A. 2009. A taxonomic revision of *Eucalyptus camaldulensis* (Myrtaceae). *Australian Systematic Botany* **22**, 257-285.

Melzer, A. 1994. Aspects of the ecology of the koala (*Phascolarctos cinereus*) in the semi-humid woodlands of Central Queensland. PhD thesis, The University of Queensland.

Munks, S.A., Corkrey, R. and Foley, W.J. 1996. Characteristics of arboreal marsupial habitat in the semi-arid woodlands of northern Queensland. *Wildlife Research* 23, 185-195.

Nagy, K.A. and Martin, R. 1985. Field metabolic rate, water flux, food consumption and time budget of koalas, *Phascolarctos cinereus* (Marsupialia: Phascolarctidae) in Victoria. *Australian Journal of Zoology* **33**, 655 - 665.

Pfeiffer, A., Melzer, A., Tucker, G., Clifton, D. and Ellis, W. 2005. Tree use by koalas (*Phascolarctos cinereus*) on St Bees Island, Queensland - Report of a pilot study. *Proceedings of the Royal Society of Queensland* **112**, 47-51.

Specht, R.L. and Specht, A. 2002. *Australian plant communities; dynamics of structure, growth and biodiversity* (Oxford University Press).

Sullivan, B.J., Baxter, G.S. and Lisle, A.T. 2003. Low-density koala (*Phascolarctos cinereus*) populations in the mulgalands of south-west Queensland. III. Broad-scale patterns of habitat use. *Wildlife Research* 30, 583-591.

Sullivan, B.J., Baxter, G.S., Lisle, A.T., Pahl, L. and Norris, W.M. 2004. Low-density koala (*Phascolarctos cinereus*) populations in the mulgalands of south-west Queensland. IV. abundance and conservation status. *Wildlife Research* **31**, 19-29.

Tucker, G., Melzer, A. and Ellis, W. 2007. The development of habitat selection by sub-adult koalas. *Australian Journal of Zoology* **55**, 285-289.

APPENDIX I

Linear koala habitat associated with creek systems and consisting of *Melaleuca* and *Eucalyptus* species near Clermont in central Queensland.

Photo, W. Ellis.

Eucalyptus crebra dominated woodland adjacent to Blair Athol Coal Mine provides habitat for koalas in central Queensland.

Photo, W. Ellis.

William Ellis and koala displaying numbered tag that provides researchers with long term identification for koalas at Blair Athol Coal Mine in central Queensland.

Photo, J. Wimmer.

Koala in *Eucalyptus crebra*, wearing VHF tracking collar.

Photo, W. Ellis

Central Queensland koala.

Photo, W. Ellis